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RELATIONS OF THE TEMPERATE FLORAS OF NORTH AND SOUTH AMERICA

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THE DISTRIBUTION of the existing land floras of the world, as well as their fossil record, have been studied by many botanists for a long time. These botanists have been, for the most part, Europeans or Americans, and have especially studied the floras of the Northern Hemisphere; and the history of the Holarctic vegetation is fairly well known. There is much less information concerning the history of the floras of the Southern Hemisphere, especially the fossils. Since we now have as allies most of the South American countries, it might be well for us to become better acquainted with the botanists of South America and their studies of the floras of those countries.

Great changes have occurred during past ages in the distribution of land and water of the globe; and great mountain ranges now stand where once the sea covered the land. These changes in the distribution of the main bodies of land and water have undoubtedly had much to do with fluctuations of climate and the distribution of many plants.

Thus the invasion of the sea in the Cretaceous Age over much of the western United States, and later, the elevation of the Rocky Mountains and the Sierra Nevada and Cascades, had a very marked effect on the climate of those regions and the distribution of the vegetation. During the Mid-Tertiary, for example, the redwood (Sequoia) now practically restricted to California, occurred over much of North America and Eurasia, and the southern cypress (Taxodium) now confined to the southeastern States was equally widespread.

The great Pleistocene glaciation caused a great redistribution of the floras

of North America and Eurasia, and many American trees, like the tulip tree (*Liriodendron*), magnolia and walnut, before the Ice Age lived also in Europe but were completely exterminated there at that time.

EXISTING FACTORS IN DISTRIBUTION

Among the factors of prime importance in the distribution of the existing floras, the first is, perhaps, the relations of the great continental masses to each other, and to the surrounding oceans. The latter are effective barriers to the migration of all but a very few plants, and high mountains and extensive areas of desert and arid regions such as occur in the center of the continents, also are barriers to migration; but mountains may also serve as highways—as may be seen in the occurrence of arctic and sub-arctic species in the Sierra Nevada and Rocky Mountains, far south of their normal habitat, and many plants are common to Chile and California.

The major part of the land surface of the globe is in the Northern Hemisphere and comprises North America and Eurasia. It is generally recognized that these two continents have for a very long time been more or less intimately connected. This is indicated by the evident close relationship of their floras, especially in the higher latitudes. Throughout the Arctic and Subarctic Zones most of the trees, shrubs and herbaceous species are closely related, or even identical. It has even been proposed to consider North America and Eurasia as parts of an ancient primary continent, "Laurasia."

The southern continents, South America, Africa, Australia and Antarctica, are separated from each other by the width of the great oceans. Except for Antarctica which is destitute of terrestrial vegetation, the southern continents have varied and peculiar floras, indicating a long period of isolation. Nevertheless they all have many obviously related genera, and even species, pointing to some ancient land connections.

It has been held by some geologists that in the late Palaeozoic there existed a great southern continent, "Gondwana," which included all the existing southern continents, and also India. Gondwana was separated from the northern land-masses by a broad oceanic belt, the "Tethys Sea" which persisted to near the end of the Mesozoic. This perhaps explains the radical differences between the present temperate floras of North and South America.

How the existing southern continents became so completely isolated has caused much speculation. In a recent study of the subject by a South African geologist,[1] the author concludes that Gondwana split into segments which drifted apart and developed into the present continents. This theory of Continental Drift, put forward by Wegener in 1912, is a plausible explanation of many puzzling facts in geographical distribution, both of animals and plants.

The greater part of North America and Eurasia lies north of the Tropic of Cancer, and extends beyond the Arctic Circle. Almost the whole of the United States lies in the "Temperate" Zone, between 30° and 50° N. For the most

[1] Our Wandering Continents. A. L. Du Toit: London, 1937.

part the climate is distinctly "continental," with great annual range of temperature. In general, winter is a season of complete cessation of plant activity. In the United States milder climates prevail in the Southern States and especially on the Pacific Coast, where weather conditions are very different from those over most of the country. From Sitka to San Diego, the climate is remarkably equable. The January isotherm of 0°C, which on the Atlantic Coast is in the region of New York and Philadelphia, on the Pacific Coast is pushed north to Sitka (lat. 57° N.). In San Francisco, there is only a difference of ten degrees Fahrenheit between the coldest and warmest months (50° to 60°); in Washington, D.C., about the same latitude (32° to 78°).

The lofty barrier of the great Cordillera protects the coastal areas from the great temperature fluctuations of the interior regions, and the prevailing westerly winds from the Pacific have a great influence on both temperature and precipitation.

In the strictly arctic regions, *e.g.*, Greenland, northern Canada and Alaska, trees are absent and the vegetation is made up for the most part of perennials, either herbaceous species with subterranean roots or root-stocks which during the brief growing season of perhaps two months, complete their season's growth; or a few woody species, *e.g.*, dwarf willows and birches, dwarf rhododendrons, cranberries and a few other bog-plants may be found. In specially favorable places Iceland poppies, buttercups, saxifrage, with showy flowers, as well as some grasses, quickly develop from their perennial roots during the very brief summer months.

Further south in the Sub-arctic Zone, trees begin to play an important role. Thus in Canada, Scandinavia, Russia, there are extensive forests of spruce and pine, birches, willows and poplars and various deciduous shrubs, much the same throughout, from Alaska to Russia.

The Sub-arctic merges gradually into the North Temperate which occupies much of North America and Eurasia. In the United States, especially in the eastern portion, this zone is characterized by an extraordinary variety of deciduous trees—oaks, beech, ash, elm, walnut, hickory, chestnut, and many others, which occur over most of the region east of the Mississippi.

About two-thirds of the United States lie between the Rocky Mountains and the Atlantic Ocean. This includes the great Mississippi Valley and the Great Lakes. The vast area between the Rocky Mountains and the Appalachians has no barriers to plant migration except climatic ones, *e.g.*, temperature and rain-fall, and many species are distributed over most of the area. Thus several species of oak, the black walnut and American elm occur over most of the area eastward of the Rocky Mountains, except where the moisture is insufficient.

The rainfall decreases westward and the forest gives way to the prairies. West of the Mississippi trees usually occur only along streams. The prairies finally pass into the semi-arid steppes which occur at the base of the Rocky Mountains. These plains are characterized by scattered bunch grasses and low shrubs, together with some herbaceous species.

The western third of North America is very different from the East. It is a region of mountains and elevated plateaus between the Rocky Mountains and the Pacific Coast. This region includes extensive plateaus and secondary mountain ranges. Much of the plateau region is arid and in some places, as in the Salt Lake region, and parts of Nevada, true deserts.

The great Pacific Cordillera which, with few breaks, extends from Alaska to Patagonia, sharply sets off the Coastal Region from the rest of the Continent. The whole of the western Mountain area is very different climatically and floristically from Atlantic North America, and is the only portion of the United States in which the highest mountains have perpetual snow and a true alpine flora.

Southern California and western Mexico have very light rainfall and much of the country is desert, but the precipitation increases rapidly northward, and in northwestern California the rainfall is very heavy; and from central California northward through Oregon, and Washington to Alaska, there is heavy rainfall, resulting in the development of the greatest coniferous forest in the world.

In the Gulf region, especially Florida, there are many types, like the palms, *Ficus* and Bromeliads, evidently derived from the tropical regions to the south.

Central California is a meeting ground for the boreal floras of North America and the subtropical floras of Mexico. There is also a considerable number of genera and even species common to California and central Chile.

The coastal ranges of central California, with their cool, moist forests, contain many distinctly boreal types, like most of the conifers, as well as such deciduous trees as maples, oaks and alders, and deciduous shrubs, honeysuckle, roses, elder, spiraea, azalea, rhododendron, dogwood, and others, and many characteristic herbaceous flowers, *e.g., Trillium, Erythronium, Ranunculus, Oxalis,* saxifrage, *Aquilegia,* violets, and many others.

With decreasing precipitation southward, these northern types are gradually replaced by genera and species absent from the eastern States, or only occasionally found, *e.g., Acacia,* cacti, *Yucca, Prosopis, Mimulus, Penstemon, Castilleja,* and others.

The occurrence in California of a considerable number of species found also in Chile is remarkable. Among these may be noted *Fragaria chilensis, Prosopis juliflora, Mesembryanthemum acquilaterale, Calandrinia Menziesii.*

The temperate regions of South America include a small part of southern Brazil, Paraguay, Uruguay, Argentina, and Chile; the two latter comprise the greater part of temperate South America. Between Chile and Argentina is the great barrier of the Andes, a condition similar to that separating the coastal region of California from Nevada and Arizona, and there is much the same difference between the coastal and inland climates in both cases, as well as in the vegetation.

The central and southern parts of Chile have abundant rainfall, while in

most of Argentina the precipitation is scanty, and much of the country is a desert. The continent diminishes in breadth southward, its southernmost point, Cape Horn, being less than 60°S.

Owing to the proximity of the oceans, the climate is insular rather than continental, and there is nothing comparable to the Arctic Zone of the northern continents. Similar conditions prevail in temperate South Africa and Australia, where the southernmost regions are under 50°S. Excepting in the high mountains there is no such difference between winter and summer as exists in corresponding latitudes in the Northern Hemisphere. Thus in Ushuaia, in Tierra del Fuego (lat. 55.5°S) the coldest monthly average is 28.9°F, the warmest 50°; at Nain (Labrador) in about the same latitude North, the range is –7°F to 46°; in Buenos Aires (lat. 35.5°S) the coldest month is 50°F, the hottest, 73.6°. St. Louis, about the same latitude North, has the range of 31° to 79.1°.

As a whole the temperate floras east of the Andes are very poor compared with corresponding areas in North America. While the flora of Argentina is mainly related to the Brazilian regions to the north, there are also elements related to those of Chile, especially in the extreme south, where there is abundant rainfall, and where the so-called "Subantarctic" flora becomes evident. This flora is also related to that of New Zealand and South Australia.

The transition from southern Brazil to Argentina is a gradual one with increasing aridity southward. The strip at the base of the Andes is very dry, with scanty vegetation, and might be compared to the most extreme deserts of Arizona and Nevada. It has been described as one of the most dismal and sterile regions that one could imagine. The precipitation increases somewhat toward the east, and much of central Argentina is occupied by the great pampas, recalling the great plains of the central United States, and like the prairies there is a great development of grasses and other herbaceous plants. The constituents of the pampas floras are for the most part quite different species from those in North America. In general the flora of northern Argentina is evidently related to that of southern Brazil.

Southward the pampas merge into the arid, sterile plains of Patagonia, where only such scanty vegetation is found as can survive the stony, exposed, and excessively dry conditions which prevail.

The conditions in Chile, west of the Andes, are very different from those in Argentina. The coast of Chile extends from 16° 57′ S to 55 S (the southernmost point in South America—Cape Horn). This corresponds to the north Pacific Coast from Lower California to Alaska.

The northern coast of Chile is practically rainless, and much of the region is quite destitute of vegetation. Passing southward, the precipitation gradually increases, and in the central region, *e.g.*, Valparaiso, Santiago, conditions are very similar to those in Central California, and the general character of the vegetation, both native and cultivated, is very much the same.

Trees and shrubs from California, *e.g.*, *Sequoia*, Monterey Cypress, *Ceano-*

thus, are planted in the parks and gardens, and the California poppy (*Eschscholtzia*) is quite naturalized. In California the Chilean pepper tree (*Schinus molle*), and *Araucaria imbricata,* are familiar trees, and *Escallonia* spp. and *Buddleia globosa* are common ornamental shrubs.

Central Chile, both in climate and topography, much resembles the corresponding regions in California, and the great central valley between the Andes and the Coast ranges may be compared with the great central valley of California. Santiago (lat. 35°S), the capital, resembles almost exactly in its rainfall and mean temperature, San Jose (lat. 37°N) in the Santa Clara Valley of California.

The rainfall in southern Chile is very heavy and there is present a luxuriant rain forest very much as the heavy coniferous forest is developed on the northern Pacific Coast. The constituents of these forests are very different; while the northern Pacific forests are composed almost exclusively of conifers—redwood, spruce, fir, hemlock, etc.; conifers are relatively rare in the Chilean forests and are all different from the northern genera, and are most nearly related to those of New Zealand and Australia. The rain forest of Chile is mostly composed of broad-leaved evergreens, mostly lacking in the northern forests. and includes many genera common to New Zealand, *e.g.,* evergreen beech (*Nothofagus*), *Drimys* (Magnoliaceae), *Laurelia* and *Weinmannia,* both important genera in New Zealand, and also *Fuchsia* and *Griselinea.* Characteristic of the forests of the South Temperate Zone are many species of the Myrtle family, almost completely absent from the North Temperate Zone, *Eucalyptus* from Australia being perhaps the best known example. Another exclusively southern family, Proteaceae, especially developed in South Africa and Australia, is well represented in South America. *Embothrium* and *Lomatia* occur in Chile.

While there is nothing corresponding to the Arctic Zone of the Northern Hemisphere, southern Chile has a flora which is unmistakably related to that of New Zealand and southern Australia. This flora has been called "Subantarctic" and indicates some former land connections with New Zealand and southern Australia.

While, in general, there is nearly a complete absence in South America of characteristic North American genera and species, in the Pacific Coastal Region there is a remarkable number of genera and even species common to Chile and central and southern California, and the adjacent southwestern areas. These may be explained as due to migration along the great mountain system of the Pacific Coast, subsequent to the union of South America and Central America.

Some of these are cosmopolitan types—like *Caltha, Linum, Geranium, Oxalis,* but a considerable number are species common to California and Chile but unknown elsewhere, *e.g., Fragaria Chilensis, Calandrinia Menziesii, Lupinus microcarpa, Madia sativa, Plantago magellanica, Gilia pusilla, Prosopis juliflora.*

Fossil Evidence

While the fossil record is necessarily incomplete it has added much to our knowledge of the history of the higher plants, especially in North America and Eurasia.

The fossil remains of plants are restricted largely to such parts, *e.g.*, stems, leaves, roots, as have firm tissues, resistant to decay. Occasionally the tissues, even the more delicate ones, are replaced by infiltration of mineral substances, lime or silica, which replace the organic matter of the cell-walls, and result in petrifactions; but as a rule the more delicate organs, such as the flowers, are very seldom found as fossils.

Much has been learned of the fossil floras of the geological eras, from the Devonian where the earliest certain remains of land plants have been found, to the Mesozoic and Tertiary formations, which contain many remains of plants, evidently closely related to living species.

From a study of these ancient fossils it is evident that as a whole plants are very conservative, and a remarkably large number of forms have come down from a very remote past to the present with little change. The common "horsetail" (*Equisetum*) and the "club-mosses" (*Lycopodium*) are very similar to some of their relations from the Carboniferous, and many fossils of the modern flowering plants (Angiosperms) as far back as the Cretaceous, when they are first certainly recognizable, can be referred to such living genera as sycamore (*Platanus*), sassafras, oak, poplar, and many others. It is to be expected that many common herbaceous plants which now are associated with these woody species also existed, but owing to their delicate perishable tissues have not survived as fossils.

Many of these fossils occur in regions now unsuited to their growth, showing that great climatic changes have taken place. Thus among the earliest Angiosperms that have been found were some described from Greenland, from rocks supposed to be of Cretaceous age. These fossils represent genera now found in regions many degrees southward. Among these fossils were sycamores, magnolias, cinnamon, and others. Sycamore (*Platanus*) is now represented in the United States by two species, one occurring from New England to the Mississippi, the other in central and southern California. It is hard to imagine any possible conditions of climate in which these trees could have grown, within a few hundred miles of the North Pole, deprived of sunlight for many months. A similar problem is offered by fossils found near the Antarctic.

While our knowledge of the fossil floras of South America is much less complete than that of North America, there have been some important contributions, especially Professor E. W. Berry's studies in the Tertiary floras of Argentina (Tertiary Flora from the Rio Pichileufu, Argentina, *Proc. U. S. Nat. Museum*, Vol. 72, 1928).

This flora includes elements now belonging to the present subtropical floras of Brazil, Paraguay, and also genera now confined to the extreme south of

Patagonia, Tierra del Fuego, and Chile, representing the "Subantarctic" regions. This indicates that the Tertiary climate in Patagonia was both warmer and more humid than at present. There were no North American genera present, but the most remarkable case was Ginkgo, unknown elsewhere in South America.

A recent study of fossil conifers from Chile (The Tertiary Fossil Conifers of South Chile and their Phytogeographical Significance) by Rudolph Florin, Stockholm, 1940, shows that the genera were the same as now exist, and that none of the characteristic North American genera, *e.g., Pinus, Abies, Tsuga, Picea,* were present. Florin states that the same complete separation of the northern and southern types has existed since the late Palaeozoic.

From a study of the existing floras as well as the fossil forms, one may conclude that the floras of South America have developed independently, except for the so-called "Subantarctic" floras, which probably originated in some common land-mass, perhaps the hypothetical Gondwana. This seems much more likely than that they originated in some northern extension of the present Antarctica.

Acceptance of the recent hypothesis of Du Toit, that there were two primordial continents, Laurasia in the Northern Hemisphere and Gondwana in the South, and from these primary continents, the existing continents were separated and shifted to their present positions, would, if true, remove most of the difficulties in explaining the present distribution of many existing plant families.